THE INDEX OF FOLIAR TRANSPIRING POWER AS AN INDICATOR OF PERMANENT WILTING IN PLANTS

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(WITH ONE FIGURE)

The index of transpiring power as put forward by LIVINGSTON[1] is taken as a measure of the power of leaves to supply moisture to the surrounding air. The reciprocal of this index is a measure of the power of leaves to retain water against the drying influence of the surroundings. The index of transpiring power for any leaf as found by means of cobalt chloride paper represents the power of the leaf to give off water, this being measured in terms of the similar power possessed, at the same temperature, by a saturated blotting paper surface blanketed by a millimeter of air. The index for an entire leaf is obtained by averaging the indices obtained for the two leaf surfaces. Indices less than unity represent leaf surfaces with lower power of giving off water than is possessed by the standard evaporating surface. Those greater than unity can give off water faster than does the standard surface at the same temperature. The work of BRIGGS and SHANTZ,[2] that of CALDWELL,[3] and that of SHIVE and LIVINGSTON[4] have recently brought forth the concept of permanent wilting in plants. This is that stage of progres-

[1] LIVINGSTON, B. E., The resistance offered by leaves to transpirational water loss. Plant World 16:1–35. 1913.

[2] BRIGGS, L. J., and SHANTZ, H. L., The wilting coefficient and its indirect determination. BOT. GAZ. 53:20–37. 1912.

———, The relative wilting coefficient for different plants. BOT. GAZ. 53:229–235. 1912.

———, The wilting coefficient for different plants and its indirect determination. U.S. Dept. Agric., Bur. Pl. Ind. Bull. 230. 1912.

[3] CALDWELL, J. S., The relation of environmental conditions to the phenomenon of permanent wilting in plants. Physiol. Res. 1:1–56. 1913.

[4] SHIVE, J. W., and LIVINGSTON, B. E., The relation of atmospheric evaporating power to soil moisture content at permanent wilting in plants. Plant World 17: 81–121. 1914.

sive wilting at which the plant cannot recover turgidity if inclosed for 24 hours (without watering of the soil) in a chamber of saturated air. Interest in this stage of wilting centers mainly about the determination of the residual moisture content of the soil at the time when permanent wilting is attained. It is unnecessary here to review the important contributions already made in this connection, but it may be safely stated that the concept of permanent wilting promises to be of great importance in soil moisture studies for ecological and agricultural interpretation. Besides the authors above mentioned, ALWAY[5] has studied the relation of plants to soil moisture, with results bearing upon this general question.

It is somewhat difficult to determine just when the stage of permanent wilting is attained; an observer can never be quite sure whether a plant is permanently wilted or not until after the 24-hour exposure in the moist chamber, and there is always considerable danger that the wilting may be carried too far. This difficulty suggested to the writer the possibility of employing the cobalt chloride paper test of foliar transpiration power as an indicator of attainment of permanent wilting.

In the summer of 1913, at the Desert Laboratory of the Carnegie Institution, some preliminary studies were carried out upon the relation of the index of foliar transpiring power to the stage of wilting in plants. It was the writer's privilege to carry out these tests upon plants actually employed in the work of SHIVE and LIVINGSTON, then in progress. The results of some of these tests have already been published.[6] They clearly indicate a direct relation between the value of the index and the extent of wilting.

During the summer of 1914 it was again the writer's privilege to carry out studies in this connection at the Desert Laboratory, and he wishes here to express his appreciation of the kindness of Dr. D. T. MACDOUGAL, director of the Department of Botanical Research of the Carnegie Institution, in placing at his disposal the facilities of the Laboratory. At the suggestion of

[5] ALWAY, A. J., Studies on the relation of the non-available water of the soil to the hygroscopic coefficient. Nebraska Agric. Exp. Sta. Research Bull. 3. 1913.

[6] BAKKE, A. L., Studies on the transpiring power of plants as indicated by the method of standardized hygrometric paper. Jour. Ecol. 2:145–173. 1914 (see pp. 166–168).

Professor B. E. LIVINGSTON, an attempt was made to obtain further information concerning the march of the wilting process by means of cobalt chloride paper and the index of foliar transpiring power.

Various writers have shown that the transpiration rate falls suddenly with wilting, but rises again thereafter to a considerable extent, subsequently to fall once more as desiccation finally occurs. It appeared that these alterations in the transpiration rate must be due to internal conditions (within the plant), and that a similar march should be shown by the value of the index of transpiring power. To test this supposition, sunflower plants (*Helianthus annuus* L.) were lifted from the open soil in the forenoon, the adhering soil was shaken from the root system, and the plants were allowed to wilt in the laboratory. The temperature of the room was about 32° C. and varied but little during the experiments. Determinations of the index of transpiring power for both the upper and lower leaf surfaces were made at hourly intervals, the first determination just preceding the lifting of the plant.

An example of the sort of results obtained is given in table I. Five leaves of different ages were employed, the same leaves being tested at each time of observation. Although there were considerable differences in the indices for different leaves at any one time, according to their various ages or positions upon the plant, all five indices have been averaged to give a single index for each time. The first observation was made just before the plant was lifted from the soil. No wilting was apparent at this time. The last observation was made after drying of the leaves became pronounced. It required 10–15 minutes to complete each observation, the tests being begun at the time indicated in the table.

From the data given in table I it is at once clear that the indices first decrease rapidly, then increase, and then decrease again. This march for the upper and lower surfaces is shown graphically in fig. 1, where abscissas denote time and ordinates denote index values which are shown upon the graphs.

Wilting began almost immediately after the removal of the plant from the soil. The indices are seen to decrease very rapidly during the first hour. This first rapid decrease is followed by a continued but very gradual decrease during the four following hours. Then a marked increase in the index values is evident, lasting for two hours, after which another decrease is clearly shown.

TABLE I

MARCH OF THE INDEX OF TRANSPIRING POWER FOR UPPER, LOWER, AND ENTIRE LEAF SURFACE OF UPROOTED PLANT OF *Helianthus annuus* L. DURING PROGRESSIVE WILTING AND DRYING OF THE LEAVES

TIME OF OBSERVATION	INDEX OF FOLIAR TRANSPIRING POWER		
	Lower surface	Upper surface	Entire surface
8:30........	0.9468	0.9020	0.9243
9:30........	0.1175	0.1289	0.1232
10:30........	0.1054	0.0865	0.0959
11:30........	0.0632	0.0699	0.0665
12:30........	0.0657	0.0616	0.0636
13:30........	0.0571	0.0578	0.0574
14:30........	0.1029	0.1013	0.1021
15:30........	0.1723	0.2029	0.1876
16:30........	0.0899	0.1216	0.1058

To interpret these alterations in the index values, it may safely be supposed that the great initial fall in the graphs represents the prompt increase in incipient drying[7] within the leaves, which must have followed the uprooting of the plant and the consequent breaking of its connection with the soil moisture films.[8] Temporary wilting had already set in before the end of the first hour.

After wilting began, the increase in incipient drying apparently continued, but at a low rate, as indicated by the gradual downward slope of the graphs for the hours 9:30 to 13:30. During this time it may be supposed that the continuous water columns[9] of the plant remained mainly intact, so that the leaves were still slowly drawing water from the stem. With increasing tension on these

[7] LIVINGSTON, B. E., and BROWN, W. H., Relation of the daily march of transpiration to variations in the water content of foliage leaves. BOT. GAZ. **53**:305–330. 1912.

[8] BROWN, W. H., The relation of evaporation to the water content of the soil at the time of wilting. Plant World **15**:121–134. 1912; CALDWELL, J. S., *loc. cit.*

[9] DIXON, H. H., Transpiration and the ascent of sap. Prog. Rei Bot. **3**:1–66. 1909; RENNER, O., Experimentelle Beiträge zur Kenntnis der Wasserbewegung. Flora **103**:171–247. 1911.

water columns the incipient drying of the leaves should be increased, which should in turn lower the transpiring power.

The relatively high transpiring power indicated for the hours 14:30 and 15:30 appears to have followed the breaking of the water columns, by which the entire water mass of the plant had previously been united. Such a breaking should remove the tensile strain from the leaf cells, decreasing the saturation deficit of their exposed cell walls and increasing their transpiring power. From the time when this rupture occurred, the removal of water from the leaves should be accompanied by air entrance and no further tensile strength could be developed. If this is the correct interpretation of the observation here set forth, the rupture of the water columns extended over the period from 13:30 to 15:30, during which time the transpiring power was markedly increasing.

After hour 15:30, it is to be supposed that practically no more water entered the leaves from the stem, and the leaves gradually dried out, exhibiting the decreasing transpiring power which should accompany desiccation.

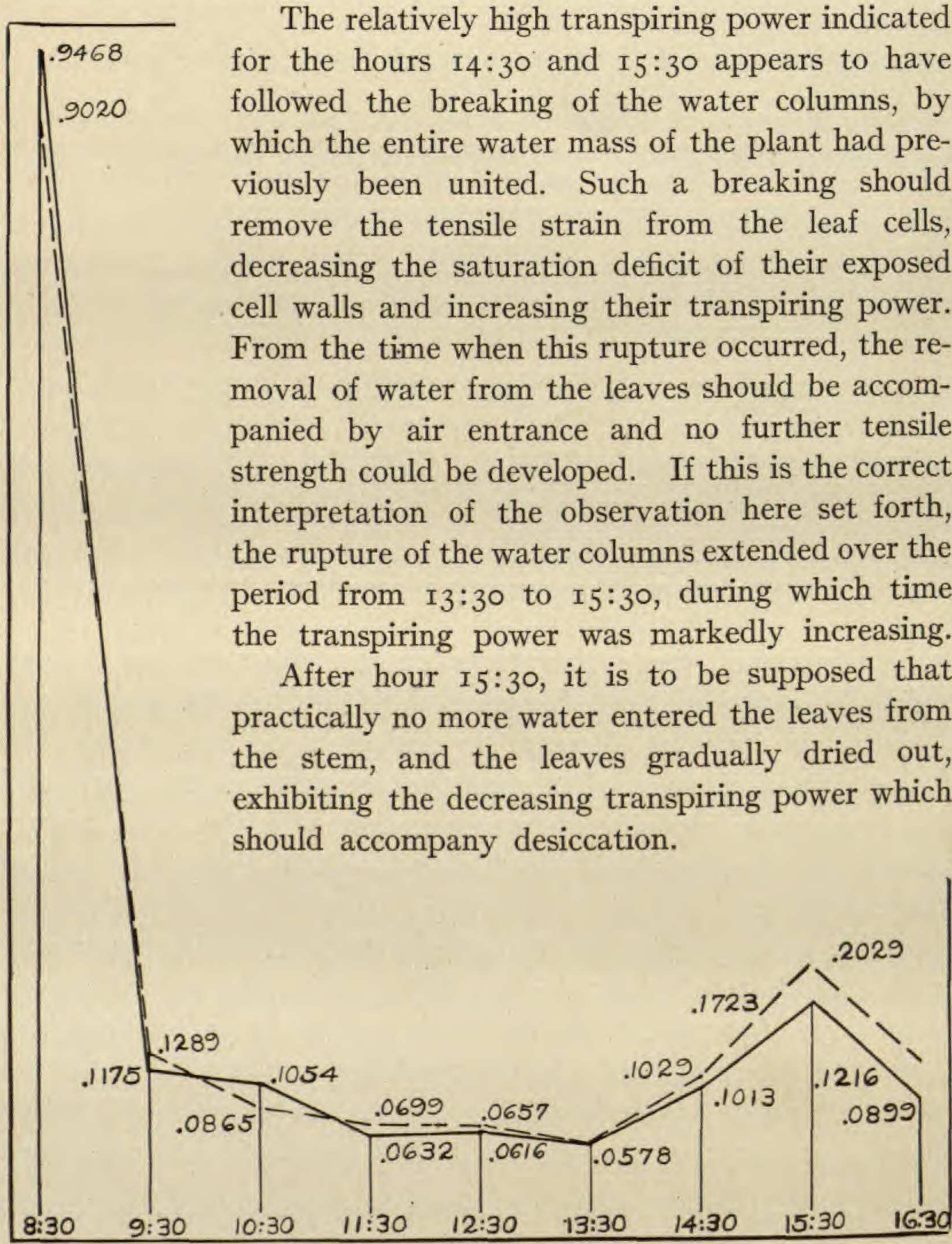

FIG. 1.—Graphs showing march of index of foliar transpiring power for wilting sunflower plant: lower leaf surface full line; upper leaf surface broken line.

From the nature of permanent wilting, and from the theoretical considerations above stated, it appears highly probable that this stage of wilting represents simply the *most intense wilting possible without serious rupture of the water columns of the plant.* At any rate, this rupture should represent a rather definite critical point in the march of the power of the plant to extract water from the soil, probably the same critical point about which the concept of permanent wilting has been developed. If this suggestion be correct, then the graphs of fig. 1 show that this critical point occurred in the particular case under discussion about hour 13:30, or five hours after the roots actually ceased to absorb moisture from the soil. In other words, it appears that the plant in question probably attained the stage of permanent wilting about five hours after it was uprooted and taken into the laboratory.

To test the validity of this supposed relation between the minimum in foliar transpiring power and the attainment of permanent wilting, it will of course be necessary to employ the hygrometric paper tests upon plants in which permanent wilting is subsequently established by the method of BRIGGS and SHANTZ—the 24-hour exposure to a saturated atmosphere, the plants being still rooted in the soil. The press of other experimentation prevented the writer from undertaking this comparison, and the foregoing suggestions have been made with the hope that such a study as that just mentioned may be accomplished at no distant time. Enough has been done to render it highly probable that the index of foliar transpiring power determined by means of cobalt chloride paper may furnish a somewhat precise criterion for the determination of that state of plants heretofore vaguely defined as permanent wilting.

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